

THE GENERA OF CAPRIFOLIACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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CAPRIFOLIACEAE A. L. de Jussieu, Gen. Pl. 210. 1789, "Caprifolia,"
nom. cons.

(HONEYSUCKLE FAMILY)

Deciduous [or evergreen] shrubs, sometimes small trees or vines, rarely herbs, with opposite [or alternate], entire or divided, exstipulate or stipulate leaves. Inflorescence a corymb, cyme, thyse, or spike of whorls, or flowers solitary or in pairs, usually bracteate and bracteolate. Flowers regular or irregular, epigynous, bisexual, rarely some sterile. Floral tube adnate to the ovary, with a distinct constriction at the level of the 3-5 usually small calyx lobes. Corolla sympetalous, 3-5-lobed, salverform, rotate, campanulate, funnelform, or tubular, often bilabiate, sometimes gibbous at or near the base; aestivation usually imbricate. Stamens 5 [4], epipetalous, alternate with the corolla lobes; filaments long or short; anthers 2-locular, longitudinally dehiscent, oblong or linear, versatile, dorsifixed, introrse or rarely extrorse; pollen tricolpate. Gynoecium 1-5-carpellate, syncarpous; style 1 or wanting; stigmas as many as the carpels, distinct or united; ovary inferior, 2-5-locular; locules with solitary to numerous, pendulous, anatropous ovules; placentation axile or parietal. Fruit a berry or drupe, rarely a capsule [or achene], 1-5-locular, with 1-∞ seeds or as many stones (pyrenes, nutlets) as locules. Endosperm copious, solid or ruminant; embryo straight, small, situated near the

¹ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued through those in volumes 40-46 (1959-1965). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with supplementary material in brackets. References which the author has not seen are marked by an asterisk.

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hilum, radicle terete, cotyledons ovoid or oblong. (Including Sambucaceae Link, Handb. 1: 662. 1829, "Sambucinae.") TYPE GENUS: *Caprifolium* Mill. = *Lonicera* L.

A family of about 18 genera and 500 species, primarily of the North Temperate Zone but extending to the mountains of the Tropics, South America, Australia, and New Zealand; seven genera native in North America; six in our area.

Caprifoliaceae are distinguished from most other families by the syncarpous, inferior ovary and opposite leaves. The presence of stipules is probably the most useful character for distinguishing the very closely related Rubiaceae, but there are exceptions, and there seems to be no single character which separates the two families consistently. Airy-Shaw has attempted to differentiate them on the basis of the scaly buds of the Caprifoliaceae *versus* the naked buds of Rubiaceae, but there are numerous exceptions in *Viburnum*. Some authors favor uniting the two families, but Kern & Van Steenis do not think this desirable without a full investigation, since many of the genera of the Caprifoliaceae would be placed in different tribes of the Rubiaceae and the identity of the family lost. These authors have drawn attention to small but important characters common to all Caprifoliaceae: the presence of enlarging calyx lobes, a distinct constriction below the limb of the calyx, dorsifixed anthers, and the absence of colleters (glandular trichomes) which occur on the inner surface of the stipules of many rubiaceous genera. The Asiatic genera *Carlemannia* Benth. and *Silvianthus* Hook. have been assigned to both the Rubiaceae and the Caprifoliaceae, but doubtfully belong to either family (see Airy-Shaw, 1965). It is problematical whether the New Zealand *Alseuosmia* Cunn. and the New Caledonian *Pachydiscus* Gilg & Schlechter and *Memecylanthus* Gilg & Schlechter belong to the Caprifoliaceae where they have been placed. *Viburnum* and, to a lesser extent, *Sambucus* show affinities with the Cornaceae, a relationship supported by pollen morphology. These genera also appear to be related to the Valerianaceae, valerianic acid occurring in both. In addition, the leaves of *Sambucus* closely resemble those of many of the Valerianaceae. The tribe Linnaeae may also show affinities with the Valerianaceae, for *Abelia* resembles the Asiatic genus *Nardostachys* in some anatomical characters.

The Caprifoliaceae have been subdivided variously. Bentham & Hooker placed *Viburnum* and *Sambucus* together in the tribe Sambuceae HBK. ex DC. and the remainder of the genera in the tribe Lonicereae R. Br. ex DC.; and pollen morphology and biochemical studies do indeed indicate a close relationship between *Sambucus* and *Viburnum*. A better treatment, however, appears to be that of Fritsch, who separated the two, recognizing the tribes Sambuceae, Lonicereae (= Caprifolieae), Linnaeae Fritsch, and Viburneae Fritsch. Meyer had previously segregated *Diervilla* and *Weigela* as tribe Diervilleae, and Wagenitz followed this course.

Reduction in the number of carpels and ovules seems to have been a feature in the evolution of the genera of the Caprifoliaceae. The basic

chromosome numbers appear to be eight and nine, and changes in chromosome number presumably have played only a minor role in differentiation of the genera. The cytogenetics of *Lonicera* and *Viburnum* have been investigated quite extensively, but other genera have been neglected. No chromosome counts are available for *Triosteum*, *Leycesteria*, and *Alseuosmia* and few for *Symphoricarpos* (two of 16 species) and *Abelia* (two of 30 species). Pollination is primarily by insects which are attracted by the conspicuous corollas, the flowers aggregated into heads, and the usually abundant nectar.

The family is of little economic importance, aside from the many species of *Lonicera*, *Weigela*, *Viburnum*, *Leycesteria*, *Abelia*, *Symphoricarpos*, and *Sambucus* cultivated as ornamentals. *Abelia* \times *grandiflora* (André) Rehd. (*A. chinensis* \times *A. uniflora*) is one of the most widely cultivated ornamental shrubs of the southeastern United States.

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KEY TO THE GENERA OF CAPRIFOLIACEAE

General characters: *shrubs or trees, rarely herbs, mostly with opposite, exstipulate or occasionally stipulate leaves; flowers usually 5-merous, the floral tube with a distinct constriction below the limb of the calyx; gynoecium syncarpous, with a 2-5-locular, inferior ovary; endosperm copious, embryo small, straight.*

- A. Corolla rotate or subrotate, deeply 5-lobed; style very short or absent; stigmas 1-5.
- B. Leaves pinnately compound; drupe with 3-5 stones. 1. *Sambucus*.
- B. Leaves simple (sometimes lobed); drupe with 1 stone. 2. *Viburnum*.
- A. Corolla campanulate, tubular, funnelform, or bilabiate; style elongate; stigma capitate.
- C. Plants coarse, erect, herbaceous perennials; fruit a dry drupe with 3 stones. 3. *Triosteum*.
- C. Plants shrubs or woody vines; fruit a capsule, fleshy drupe, or berry.

- D. Corolla campanulate; ovary 4-locular; fruit a drupe with 2 stones.
 4. *Symphoricarpos*.
- D. Corolla funnelform, tubular, or bilabiate; ovary 2- or 3(-5)-locular;
 fruit several- or many-seeded.
- E. Ovary slender; calyx lobes linear-lanceolate; fruit a capsule.
 5. *Diervilla*.
- E. Ovary globular to ovoid; calyx lobes short-triangular; fruit a
 berry. 6. *Lonicera*.

Tribe SAMBUCEAE HBK. ex DC.

1. *Sambucus* Linnaeus Sp. Pl. 1: 269. 1753; Gen. Pl. ed. 5. 130. 1754.

Rank-smelling deciduous shrubs or small trees [rarely perennial herbs]. Stems with a large pith. Winter buds with several pairs of scales. Leaves pinnately or bipinnately compound and usually with serrate leaflets, exstipulate or stipules small [or conspicuous] or reduced to glands. Inflorescence a corymb, cyme, or thyse, usually terminal, bracteolate, the pedicels articulate at apex. Flowers small, white or yellowish, regular, bisexual. Calyx lobes 5 [3], small. Corolla rotate, 5 [3 or 4]-lobed, lobes imbricate [rarely valvate], ovate [to oblong-lanceolate]. Stamens 5, inserted toward the base of the corolla; filaments slender, subulate; an-

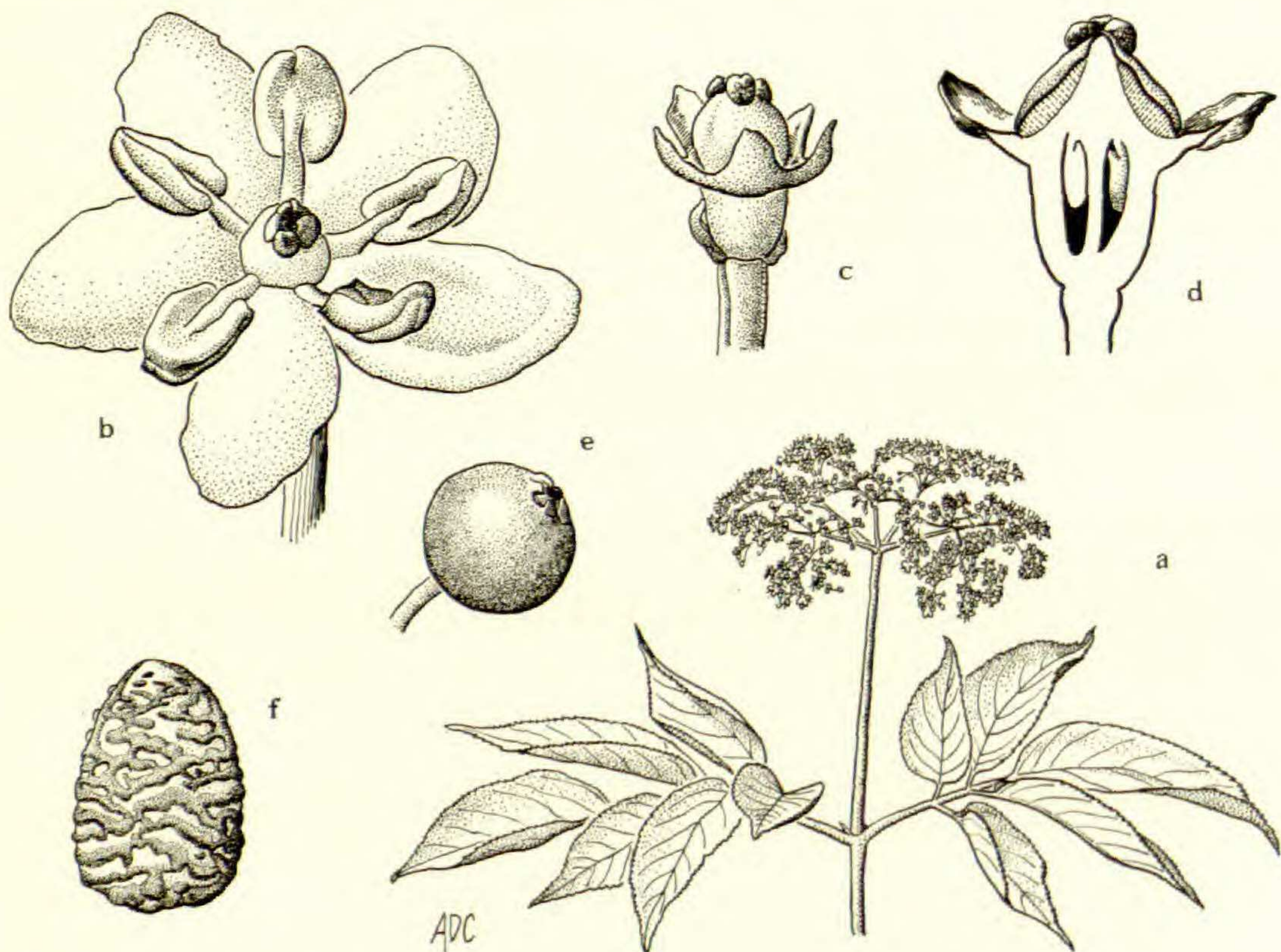


FIG. 1. *Sambucus*. a-f, *S. canadensis*: a, flowering branchlet, $\times 1/4$; b, flower, $\times 6$; c, flower with corolla and stamens removed to show bracteoles and calyx lobes, $\times 6$; d, semidiagrammatic vertical section of flower with corolla and stamens removed to show solitary, pendulous, anatropous ovule in each locule, $\times 10$; e, fruit, $\times 3$; f, stone, $\times 9$.

thers short, oblong, extrorse; pollen small to medium sized, reticulate. Stigma sessile, red or white, 3–5-lobed; ovary 3–5-locular with a solitary, pendulous ovule in each locule. Fruit a small ovoid or globular drupe with 3–5 cartilaginous, 1-seeded stones; stones oblong, compressed, rugulose or smooth. Seeds with a membranaceous testa and fleshy endosperm. Embryo sac development of the *Adoxa* type. LECTOTYPE SPECIES: *S. nigra* L.; see Britton & Brown, *Illus. Fl. No. U. S. ed. 2. 3: 268. 1913.* (Classical Latin name for the plant; believed to be from Greek, *sambuké*, a stringed musical instrument supposed to be made of the wood of the elder, *S. nigra*.) — ELDER.

A widespread genus of about 20 species, centered chiefly in the temperate regions of the Northern Hemisphere but extending south to the mountains of the Tropics and to East Africa, South America, Australia, and New Zealand; about ten species in North America, including the introduced *Sambucus nigra* and *S. Ebulus* L.; two or three species in our area.

Sambucus racemosa L. is widespread in cool-temperate regions of the Northern Hemisphere. In North America it is represented by subsp. *pubens* (Michx.) Hultén (*S. pubens* Michx.), $2n = 36$, which occurs throughout much of Canada and the northern United States and southward in the mountains to North Carolina, Tennessee, and northern Georgia. The paniculate inflorescences, red fruits, brown pith, and early spring flowering are characteristic. It is closely related to the European subsp. *racemosa*, $2n = 36$, separated by its denser inflorescences and glabrous leaves, and to the Japanese subsp. *Sieboldiana* (Miq.) Hara, distinguished by its reddish stigmas and small fruits. Some authors have treated these taxa as distinct species; their status needs further investigation.

Sambucus canadensis L., $2n = 36$, widespread in our area and extending throughout the greater part of North America, contrasts with *S. racemosa* in its umbelliform inflorescences, black fruits, white pith, and later flowering time in areas where both occur. *Sambucus Simpsonii* Rehd., a variant which occurs from the West Indies to Florida and north to southern Georgia, Alabama, Mississippi, and Louisiana, is very doubtfully distinct from *S. canadensis*. Rehder distinguished this species by its treelike habit, smooth bark, narrow pith, and usually five-locular ovary, in contrast with *S. canadensis* with shrubby habit, rough bark, wide pith, and usually four-locular ovary. Investigation of some of Rehder's material shows that the number of locules in the ovary may vary from three to five but is predominantly four. The other differences are perhaps a result of more favorable climatic conditions. Later authors have called attention to the pinnately divided lower leaflets of *S. Simpsonii*, a characteristic which is common in peninsular Florida, although northward numerous intermediates with a variable number of leaflets occur. Brown reports the frequent occurrence in Louisiana of specimens which have occasional leaves with the lower leaflets divided as in *S. Simpsonii* but with most of the leaves on the same branch like those of *S. canadensis*.

The pinnate leaves and extrorse anthers, as well as numerous small anatomical characters, make *Sambucus* a very distinct genus, but its taxonomic position is not clear. It shows affinities with *Viburnum* in floral characters, and some authors (e.g., Bentham & Hooker and Fernald) associate these genera as the tribe Sambuceae. Others (e.g., Fritsch and Wagenitz) regard *Sambucus* as constituting a separate tribe, while Höck has segregated it as the family Sambucaceae. Van Steenis has drawn attention to a marked structural resemblance between *Sambucus* and *Turpinia* Vent. and suggested that a fuller investigation should be made of the relationships between *Sambucus* and the Staphyleaceae.

Pollination is probably by insects, although few pollinators have been reported for some species and floral nectaries are absent. Both proterandry and proterogyny have been observed, and both self- and cross-pollination may occur. Chromosome numbers of $2n = 32, 36,$ and 38 have been reported.

Several species are grown as ornamentals, and ripe fruits of some, including *Sambucus canadensis*, are used for making jellies and wines. The hard wood of *S. nigra* has been used in making musical instruments, as a source of pegwood and charcoal in Europe, and in various other ways. The large pith has been used both as a cleaning agent for the pivots of delicate machinery and for holding botanical specimens in the preparation of freehand sections.

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Tribe VIBURNEAE Fritsch

2. *Viburnum* Linnaeus, Sp. Pl. 1: 267. 1753; Gen. Pl. ed. 5. 129. 1754.

Deciduous [or evergreen], erect or decumbent shrubs or small trees. Winter buds naked or with scales. Leaves membranaceous to subcoriaceous, opposite or rarely whorled, entire, crenate, dentate, or lobed, glabrous or hairy (often with stellate tomentum), petiolate, exstipulate or stipulate, or the stipules partially adnate to the petiole [or sometimes reduced to glands]. Inflorescences terminal or axillary, compound, umbel-like or paniculate, cymose; bracts and bracteoles usually small, caducous. Flowers regular, bisexual, sometimes the marginal flowers of the inflorescence radiate, slightly irregular, and neutral. Calyx lobes 5, persistent.

Corolla rotate or subrotate [to campanulate], 5-lobed, white (rarely cream or pink), imbricate in bud. Stamens 5, inserted at the base of the corolla; filaments long or short, slender; anthers oblong, introrse, 4-lobed; pollen small to medium sized, reticulate. Style short, conical, glabrous or hairy; stigma 3-lobed; ovary with 2 abortive locules and 1 fertile locule with a single pendulous ovule. Fruit an ellipsoid, ovoid, or globose, 1-seeded drupe crowned by the persistent calyx lobes and style; mesocarp with bitter or sweet flesh; stone globose or laterally compressed, oblong-elliptic to ovate, often grooved or furrowed, the edges inflexed or undulate. Seed with copious, fleshy, solid or ruminant endosperm; embryo minute, linear, situated near the micropyle. Embryo sac development normal (Polygonum type). LECTOTYPE SPECIES: *V. Lantana* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 142. 1929.² (Classical Latin name for the genus, thought to refer to *V. Lantana*; also said to be from Latin, *viere*, to bind, because of the pliability of the branches of some species.) — ARROW-WOOD.

A complex genus of about 250 species, mainly of the North Temperate Zone, but occurring south to Central and South America, Java, and Timor; approximately 25 species in North America, including three naturalized from Asia; about 13 (in four sections) native in our area.

Rehder distinguished nine sections based primarily on the shape and furrowing of the stone, number of scales on the winter buds, and leaf venation. Unpublished data from studies of petiolar anatomy by R. A. Howard support the separation of some of these sections. Rehder's treatment, however, does not include the species of Central and South America and Malesia, and a full investigation of the genus is needed.

Section PSEUDOTINUS Clarke ("*Alnifolia*" Small), distinguished by the presence of radiate flowers, naked winter buds, and ruminant endosperm, includes three species of eastern Asia and one of eastern North America. *Viburnum lantanoides* Michx. (*V. alnifolium* Marsh.),³ $2n =$

² Britton (N. Am. Trees 853. 1908) apparently was the earliest author to select a lectotype species for *Viburnum*. His choice of *V. Tinus* L., also adopted by Abrams & Ferris (Illus. Fl. Pacif. States 4: 46. 1960), cannot be accepted, for *V. Tinus* is a constituent of the segregate genus *Tinus* Miller (Gard. Dict. Abr. ed. 4. 1754). Rehder (Bibliogr. Cult. Trees Shrubs 602. 1949) also gives *V. Lantana* L. as the lectotype species.

³ *Viburnum alnifolium* Marshall (*Arbustrum Americanum* 162. 1785) must be typified by the description, for there is no known Marshall specimen. This description is almost a verbatim copy of the informal English description of Miller's *V. americanum* (Gard. Dict. ed. 8. 1768) and must be considered to be the same (cf. K. K. Mackenzie, *Torreyia* 27: 81-83. 1927). The Miller specimen in the British Museum (Natural History) labeled *V. americanum* is *Hydrangea arborescens* L. in early fruiting condition. Miller's diagnosis of 1768 [*Viburnum* (*Americanum*) foliis cordato-ovatis acuminatis serratis, petiolis longissimis laevibus. *Wayfaring tree with heart-shaped, oval, acute-pointed, sawed leaves, growing upon very smooth foot-stalks*] can apply entirely to *Hydrangea arborescens*, but his further informal account can only be interpreted as a mixture of *V. lantanoides* Michx. and *Hydrangea arborescens*. In the latter Miller refers to the leaves as having long, slender petioles and "deeply sawed" edges, characters of *Hydrangea arborescens*, not *V. lantanoides*, while he

18, is widespread in cool forests of the northeastern United States and adjacent Canada and extends southward in the higher mountains to North Carolina, Georgia, and Tennessee.

Section LENTAGO DC. ("*Prunifolia*" Small, "*Obovata*" Small), represented by some six species in North America, is characterized by winter buds with one pair of scales and leaves with anastomosing veins. *Viburnum cassinoides* L., $2n = 18$, is widespread from Newfoundland to Ontario but southward is confined mainly to the mountains in the Carolinas, Tennessee, northern Alabama, and Georgia. Characteristically with obscurely dentate to denticulate leaves, grooved stones, and shortly exerted anthers, it is usually distinguishable from the closely related and more polymorphic *V. nudum* L., $2n = 18$, which has entire or only crenulate leaves, flat stones, and long filaments. *Viburnum nudum* occurs at lower altitudes throughout much of the southeastern United States, north to Kentucky and southern Connecticut, and west to Texas. The interrelationships of these species may merit further study.

Viburnum rufidulum Raf. (*V. rufotomentosum* Small), $2n = 18$, usually easily recognized by its rusty tomentum and serrate leaves and widespread throughout our area (although absent from peninsular Florida), ranges to Texas, Indiana, Illinois, Missouri, and Ohio. *Viburnum prunifolium* L., $2n = 18$, which lacks the rufescent tomentum, occurs from the Carolinas, Georgia, Tennessee, and Arkansas, north to New York and Connecticut, and west to Kansas and Texas. Some authors have regarded the populations from Arkansas and Missouri as a separate species (*V. Bushii* Ashe) or variety (var. *Bushii* (Ashe) Palmer & Steyerl.), but Steyerl. has shown that the leaf characters involved are so variable that these populations should not be treated as a distinct taxon. Some specimens seen from North Carolina appear intermediate between *V. prunifolium* and *V. rufidulum*. Another closely related species, the more northern *V. Lentago* L., $2n = 18$, has been reported from North Carolina and upland Georgia, but no confirming specimens have been found. The remaining species of the section is *V. obovatum* Walt. ("*Obovata*" Small), $2n = 18$, which has included stamens and usually small leaves. It occurs throughout most of Florida (apparently absent from the Keys), north to southern Georgia

describes the plant as eight or ten feet tall and the fruits as oval red berries. The other details of the description can apply equally well to either species.

If the *Viburnum* element in Miller's description is used to typify *V. americanum*, this unfamiliar and long unused name must be taken up in preference to either *V. alnifolium* or *V. lantanoides*. The course followed here is to continue to typify *V. americanum* Mill. (and *V. alnifolium* Marsh.) by the *Hydrangea* element and to maintain as correct under the International Code *V. lantanoides* Michx., a name which has been used for the *Viburnum* element for a long time by many authors. This procedure follows that proposed by Mackenzie (*loc. cit.*), Suringar (Mitt. Deutsch. Dendrol. Ges. 43: 216, 217. 1931), and Rehder (Jour. Arnold Arb. 28: 446. 1947) and avoids another change in the name of this very characteristic species of *Viburnum*.

I am grateful to Dr. N. K. B. Robson, of the British Museum (Natural History) for examining and commenting upon Miller's specimen of *Viburnum americanum*.

and southwestern South Carolina. *Viburnum Nashii* Small appears to be only a robust form of this species.

Section ODONTOTINUS Rehder ("*Dentata*" Small), the species of which have coarsely dentate or lobed leaves and winter buds with two pairs of outer scales, has about six North American representatives, all of which occur in our area. A careful biosystematic study of this taxonomically difficult and confused group is needed. There is no general agreement on the delimitation of the species; the treatment followed here is that proposed by Fernald. *Viburnum Rafinesquianum* Schultes var. *Rafinesquianum* (*V. affine* var. *hypomalacum* Blake), $2n = 36$, distinguished by small, short-petioled or almost sessile stipulate leaves, is widely distributed from Quebec to Manitoba and south to upland Georgia and North Carolina. The glabrous var. *affine* (Bush ex Schneid.) House (*V. affine* Bush ex Schneid.) reaches our area in Arkansas. Closely related, *V. molle* Michx., $2n = 18$ and 36 , with its long-petioled, deeply cordate leaves and flat stones, ranges from Indiana to Missouri, south to northern Arkansas. *Viburnum dentatum* L., $2n = 36, 54,$ and 72 , including *V. scabrelum* Chapm. (*V. semitomentosum* (Michx.) Rehd.) and *V. Ashei* Bush, a highly polymorphic complex characterized by rounded leaf bases, coarsely dentate leaf margins, long, usually exstipulate petioles, and hairy styles, is widespread throughout our area (except peninsular Florida) and beyond, reaching Texas and Massachusetts. *Viburnum bracteatum* Rehd., distinguished from *V. dentatum* by its long bracts and bracteoles and larger corolla, is known only from northwestern Georgia. *Viburnum recognitum* Fern., $2n = 36$, very closely related to *V. dentatum*, is considered by some authors as var. *lucidum* Ait. It is separated by its glabrous young shoots and leaves, and ranges from New Brunswick to Ontario south to the Carolinas, Tennessee, northern Alabama, and Arkansas in our area. In contrast to this difficult group, *V. acerifolium* L., $2n = 18$, throughout its wide range from Minnesota to Quebec, south to the Carolinas, northern Georgia, Tennessee, Alabama, northern Florida, and Louisiana, is immediately recognized by its palmately lobed leaves. *Viburnum densiflorum* Chapm., described from northern Florida and reported to occur in southern Georgia, Alabama, and Louisiana, appears at best to be only a variety (var. *densifolium* (Chapm.) McAtee) of this species.

Viburnum is a well-defined genus distinguished by its single-stoned drupe, usually regular flowers, nearly sessile stigma, and simple leaves. It shares with *Sambucus* regular flowers, uniovulate locules, and the occurrence of stipules in some species. Although various authors have associated the two, others have placed *Viburnum* and *Triosteum* together. A very close relationship with either seems doubtful, however, and the genus should probably be regarded as the only member of a separate tribe. *Viburnum* also shows affinities with *Abelia* and *Symphoricarpos*.

Seed germination, anatomy, and the pharmaceutical properties of the wood and bark of many species have been extensively investigated, but there is a need for further ecological information. Volatile oils and as-

sociated unpleasant odors resembling those found in *Valeriana* are characteristic.

Pollination is by insects, especially Hymenoptera and Diptera. Chromosome numbers of $2n = 16, 18, 20, 22, 27, 32, 36, 40, 48, 54,$ and 72 have been reported.

Many species are widely cultivated as ornamentals. An extract from the bark of *Viburnum prunifolium* has been used in medicine for its antispasmodic properties.

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3. *Triosteum* Linnaeus, Sp. Pl. 1: 176. 1753; Gen. Pl. ed. 5. 81. 1754.

Perennial herbs with coarse, erect, glabrous or hairy stems. Leaves opposite, entire [divided], obovate to oblanceolate to panduriform, connate or united by a ridge around the stem, sessile, exstipulate, usually hairy. Flowers bisexual, irregular, sessile, solitary or in clusters of 2-4 in the axils of leaves [or in short, terminal, whorled spikes], bracteate and sometimes bracteolate. Calyx lobes 5, linear-lanceolate, foliaceous, persistent. Corolla 5-lobed, imbricate, a little longer than the calyx, greenish yellow to dull red, tubular, usually hairy within, slightly gibbous at the base, with a nectary of sessile or very short-stalked glands. Stamens 5, inserted about halfway up the corolla tube, usually included; filaments short, hairy; anthers oblong or linear, introrse, united for most of their length; pollen medium to large, echinate. Stigma capitate, 3-5-lobed; style usually hairy below, included or shortly exerted; ovary 4-locular, 3 locules with solitary ovules, 1 empty. Fruit a dry drupe containing 3 ribbed stones with a thick, bony endocarp. Seeds with well-developed endosperm; embryo minute, situated near the micropyle. Embryo sac development normal (*Polygonum* type). LECTOTYPE SPECIES: *T. perfoliatum* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 3: 274. 1913. (Name an abbreviation of Dillenius's *Triosteospermum*, derived from

Greek, *treis*, three, *osteon*, bone, and *sperma*, seed, in allusion to the three stones; see Linnaeus's comments about sesquipedalian generic names in Crit. Bot. 133–135. 1737 [pp. 104–107 in English ed., A. Hort., transl., 1938].) — FEVERWORT, HORSE-GENTIAN.

A genus of about eleven species of the Himalaya, eastern Asia, and eastern North America; three species in North America, all occurring in our area. *Triosteum angustifolium* L., recognized by its hispid-setose indumentum, solitary flowers, and paired bracts, ranges from Connecticut to Illinois and south to the Carolinas, Tennessee, Georgia, and Alabama, and is reported to occur in Louisiana. *Triosteum perfoliatum* L. extends from Massachusetts to Wisconsin and Minnesota south to the Carolinas, Tennessee, Georgia, and Alabama. It is characterized by the lower leaves with broad connate leaf bases, soft indumentum, and 1–4-flowered inflorescences, with a single bract and paired bracteoles. Both this and the preceding seem to be associated with basic soils. *Triosteum aurantiacum* Bickn. is a polymorphic species considered to be doubtfully distinct from *T. perfoliatum* by some authors and treated as var. *aurantiacum* (Bickn.) Wiegand. Separated from the other species by the lower leaves tapering to the base, soft indumentum, shorter style, and earlier flowering time, it occurs throughout the northeastern United States, southward to the mountains of North Carolina, Tennessee, and Georgia.

Triosteum is a well-defined genus readily distinguished by its tubular corolla, herbaceous habit, and dry drupaceous fruit. Its uncertain affinities need investigation. Associated by various authors with both Viburneae and Caprifolieae (Lonicereae), *Triosteum* seems to have closer affinities with the Caprifolieae than with *Viburnum*. Fritsch thought that it probably lies between the tribes Viburneae and Linnaeae. The mode of pollination is unknown, the cytology of the genus has not been investigated, and ecological information is needed. A study of dormancy, weathering of the bony endocarp, and germination might yield interesting data.

Triosteum is of no economic importance. The dried and roasted fruits have been used as coffee. The roots of *T. perfoliatum* are a mild cathartic.

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Tribe LINNAEAE Fritsch

4. *Symphoricarpos* Duhamel, *Traité Arbres Arbustes* 2: 295. *pl.* 82. 1755.

Deciduous, erect [or decumbent] shrubs. Winter buds with 2 pairs of outer scales. Leaves opposite, usually entire but sometimes toothed or lobed, glabrous or hairy, exstipulate, short petiolate. Inflorescences terminal or axillary racemes or spikes of paired, opposite, sessile or short-pedicelled flowers [or flowers solitary]. Flowers bisexual, slightly irregular, subtended by bracts and paired bracteoles. Calyx lobes 5 [4], persistent. Corolla 5[4]-lobed, campanulate [salverform or tubular-funnelform], sometimes slightly gibbous at the base, with a nectary of sessile glands [or with 5 distinct nectaries]. Stamens 5 [4], inserted near top of corolla tube, included or exerted; filaments short, sometimes villous; anthers oblong or linear, introrse, united for most of their length; pollen echinate. Style glabrous or hairy, shorter than the corolla; stigma capitate or slightly 2-lobed; ovary 4-locular, usually with 2 fertile 1-ovulate locules and 2 sterile several-ovulate locules, the placentation axile. Fruit a globose, ovoid or ellipsoid drupe with 2 more or less compressed stones with a bony endocarp. Seeds oblong; endosperm copious, fleshy; embryo minute. Embryo sac development normal (Polygonum type). TYPE SPECIES: *Lonicera Symphoricarpos* L. = *S. orbiculatus* Moench. (Name from Greek, *symphorein*, to bear together, and *karpos*, fruit, in allusion to the clustered fruit.) — SNOWBERRY.

A genus of about 15 species of North America, two occurring in our area, and *Symphoricarpos sinensis* Rehd. in central China. The species fall into two groups treated either as sections or subgenera: sect. SYMPHORICARPOS (subg. *Eusymphoricarpos* G. N. Jones), in which the lobes of the shortly campanulate corolla are as long as or longer than the tube, and sect. MERIDIONALES Gray ex Schneid. (subg. *Anisanthus* (Willd. ex Roem. & Schult.) G. N. Jones), in which the lobes of the tubular or salverform corolla are shorter than the tube. These differences hardly seem to be of subgeneric value. Both species in our area belong to sect. SYMPHORICARPOS.

Symphoricarpos orbiculatus Moench (*S. Symphoricarpos* (L.) MacMillan), $2n = 18$, ranges from New York south to Florida, west to Texas, Colorado, and northern Mexico. The species seems to be a calciphile. The short, hairy styles and abundant small, purplish-red fruit contrast with the longer, glabrous styles and white fruit of *S. albus* (L.) Blake (*S. racemosus* Michx.). The var. *albus* is of wide range in the northern United States; the western American var. *laevigatus* (Fern.) Blake (*S. rivularis*

Suksdorf), widely cultivated as an ornamental shrub, is sporadically naturalized in our area. The characters of glabrous leaves and young shoots, large berries, and erect habit used to separate var. *laevigatus* from var. *albus* do not seem to be constant. Experimental studies are desirable.

Pollination appears to be chiefly by Hymenoptera. There seems to be no mechanism to limit self-pollination. Cleistogamous flowers have been reported in cultivated specimens of *Symphoricarpos orbiculatus*. The structure of the pericarp and dormancy and after-ripening of the seeds have been extensively investigated. It is reported that the root development of some species suggests a mycorrhizal association. The cytology of the genus is not well known; chromosome numbers have been reported only for *S. albus*, $2n = \text{ca. } 54$, and *S. orbiculatus*.

Symphoricarpos is usually placed in the tribe Linnaeae, which is distinguished by its four or three carpels with one-seeded fertile locules and two sterile locules. It is probably closely related to *Abelia*, in which the ovary is three-locular and the fruit an achene. It also shows affinities with *Kolkwitzia* and *Linnaea*.

A number of species, including both of ours, are cultivated as ornamentals.

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Tribe DIERVILLEAE C. A. Meyer

5. *Diervilla* Miller, Gard. Dict. Abr. ed. 4. 1754.

Deciduous, erect, often stoloniferous shrubs. Winter buds with several pairs of pointed scales. Leaves opposite, entire or serrate, glabrous or hairy, sessile or short petiolate, exstipulate. Inflorescence of terminal or axillary 3- to several-flowered, short-pedunculate, bracteate cymes sometimes forming a terminal thyrses. Flowers bisexual, slightly irregular, short pedicelled, bracteolate. Floral tube slender; calyx lobes 5, linear-lanceolate, persistent or deciduous late in fruit. Corolla 5-lobed, bilabiate, with a 4-lobed upper lip, the lower lip and inner surface of the funnelliform tube densely hairy; tube slightly gibbous at the base, with a large sub-globular nectary. Stamens 5, inserted near the top of the corolla tube; filaments pubescent; anthers linear, usually exerted, introrse, dorsifixed, anther-halves free at the base, united above; pollen medium to large, echinate. Stigma capitate; style long, slender, densely pubescent below, equal in length or a little longer than the tube; ovary elongate, 2-locular, with numerous ovules, placentation parietal. Fruit a thin-walled septicidal capsule very weakly or tardily dehiscent, bivalvate, crowned with the persistent calyx. Seeds small, ovoid, with a reticulate testa; endosperm

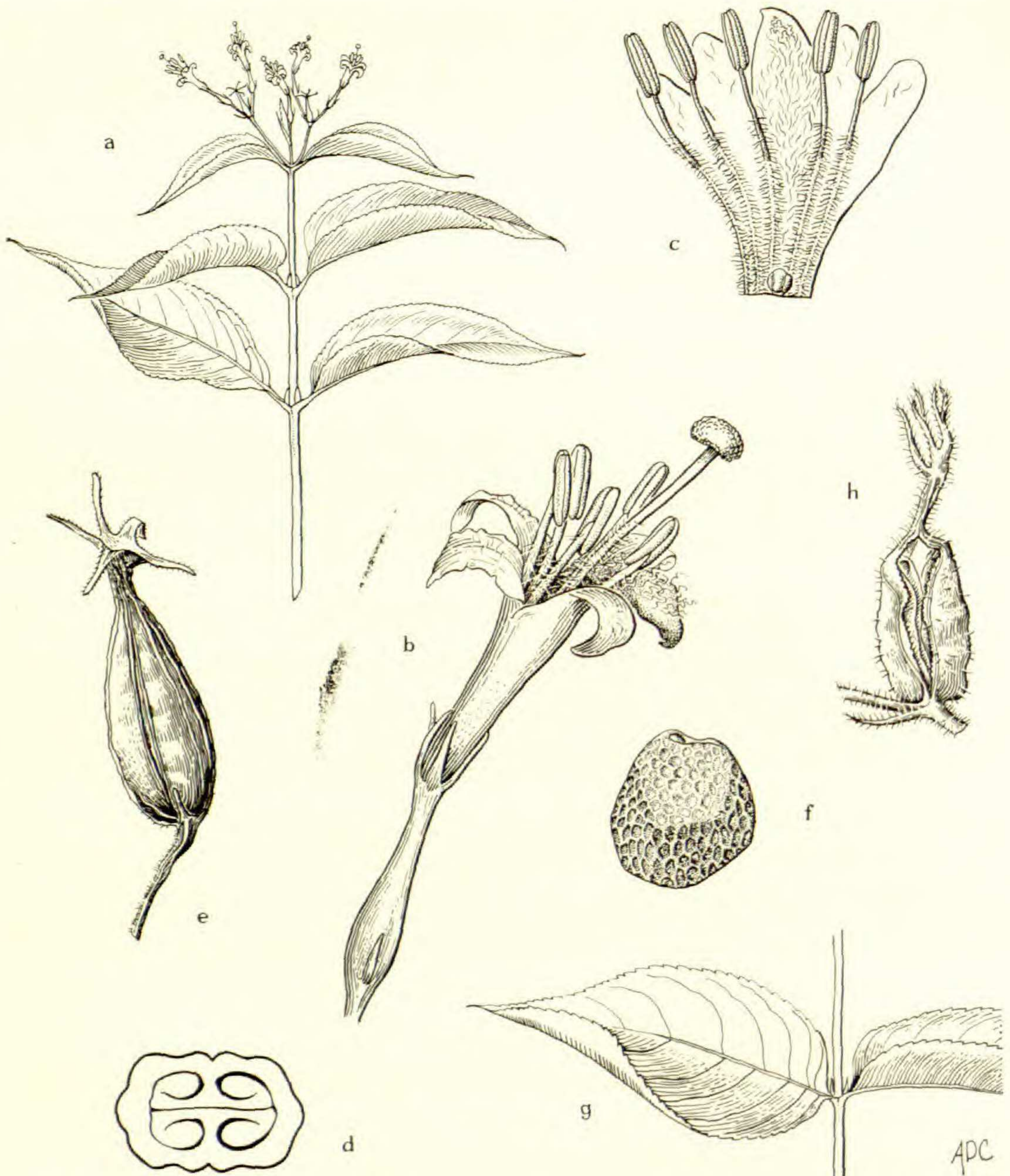


FIG. 2. *Diervilla*. a-f, *D. Lonicera*: a, flowering branchlet, $\times 1/2$; b, flower, $\times 3$; c, corolla opened lengthwise to show attachment of stamens, distribution of hairs, and subglobular nectary, $\times 2\ 1/2$; d, ovary in semidiagrammatic cross section to show parietal placentation, $\times 20$; e, capsule crowned with persistent calyx, $\times 4$; f, seed, $\times 24$. g, *D. sessilifolia*: node with sessile leaves, $\times 1/2$. h, *D. rivularis*: dehiscent capsule to show two valves and persistent calyx, $\times 3$.

fleshy; cotyledons large, superior. Embryo sac development normal (*Polygonum* type). TYPE SPECIES: *Lonicera Diervilla* L. = *D. Lonicera* Mill. (Named after Diéreville or Dierville, a French surgeon who traveled in eastern Canada (Acadia), 1699–1700, and introduced the plant into France.) — BUSH-HONEYSUCKLE.

A genus including either three species of eastern North America or about

12 more of eastern Asia, depending upon the generic concept. *Diervilla Lonicera*, $2n = 18$, characterized by its petiolate rather than sessile leaves, occurs from Newfoundland to Saskatchewan, southward in the mountains to North Carolina and Tennessee. *Diervilla sessilifolia* Buckl., $2n = 36$, of mountain woods in North Carolina, Tennessee, Georgia, and Alabama, is distinguished from the closely related *D. rivularis* Gattinger (*D. sessilifolia* var. *rivularis* (Gattinger) Ahles), $2n = 36$, which occurs over about the same range, by its longer capsules and glabrous leaves.

The flowers are reported to be proterogynous and are adapted for pollination by Hymenoptera. The color of the corolla changes in the North American species from yellow to orange or red after anthesis.

The generic concept of *Diervilla* has been varied. A distinctive group of Asiatic species has been treated as a separate genus, *Weigela* Thunb., or as either a section (*Weigela* (Thunb.) Koehne) or subgenus (*Weigela* (Thunb.) K. Koch) of *Diervilla*. The Asiatic species are characterized by large, regular, pink to red corollas, woody capsules with a well-developed columella extending beyond the ends of the valves, and seeds with short wings, with the exception of the Japanese *W. Middendorffiana* Verschaffelt, which differs in its yellow corolla, capsule without a well-developed persistent columella, irregular bilabiate calyx, pilose anthers connected by hairs in a ring about the style, and long-winged seeds. This last species has been variously treated as a separate genus, *Macrodiervilla* Nakai, or as sect. *Calyptrostigma* Koehne of *Diervilla*. Another Japanese species, *W. Maximowiczii* (S. Moore) Rehd., intermediate in its yellow flowers, pilose anthers connected in a ring about the style, and capsule with a short, persistent columella equal in length to the valves, has also been treated as a separate genus (*Weigelastrum* (Nakai) Nakai) or as a section (*Weigelastrum* Nakai) of *Diervilla*. Further investigation is needed to determine the status of these groups.

Both *Diervilla* and *Weigela* have affinities with *Lonicera*, *Leycesteria*, and *Abelia*.

Species of *Weigela* are important as ornamental shrubs; the small-flowered North American species of *Diervilla* are rarely cultivated.

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Tribe CAPRIFOLIEAE [Lonicereae R. Br. ex DC.]

6. *Lonicera* Linnaeus, Sp. Pl. 1: 173. 1753; Gen. Pl. ed. 5. 80. 1754.

Deciduous or, more rarely, evergreen shrubs or woody climbers. Winter buds with several or 2 outer scales. Leaves usually entire, sometimes lobed or pinnatifid when young, opposite, short petiolate, sessile or connate, sometimes glaucous, glabrous or hairy, exstipulate. Inflorescence of simple, 2-flowered axillary cymes or of 3-flowered cymes either axillary or aggregated in terminal heads or whorls, bracteate. Flowers mostly conspicuous, regular or irregular, bisexual, subtended by paired, often connate [rarely wanting] bracteoles. Calyx 5-lobed [or truncate], the limb persistent [or deciduous]. Corolla 5-lobed, bilabiate, with a 4-lobed upper lip, or regular, imbricate, tubular or funnelform with a long or short tube, sometimes gibbous and with a nectariferous area of many sessile glands at the base. Stamens 5, inserted near the top of the corolla tube; filaments long, slender; anthers oblong or linear, usually exserted, introrse; pollen medium to large, echinate. Stigma capitate; style slender, equaling or a little longer than the corolla tube; ovary 2-3 [rarely to 5]-locular with 3-8 ovules [the walls of the ovaries of 2-flowered cymes sometimes united], placentation axile, the septa becoming free toward the top of the ovary. Fruit a few-seeded fleshy berry. Seeds ovoid, with a smooth or reticulate [or granular] testa; endosperm fleshy. Embryo sac development normal (*Polygonum* type). LECTOTYPE SPECIES: *L. Xylosteum* L.; see Rehder, Bibliogr. Cult. Trees Shrubs 614. 1949.⁴ (Named in honor of Johann

⁴The lectotype species of *Lonicera* has been incorrectly cited as *L. Caprifolium* L. by Britton & Brown (Illus. Fl. No. U. S. ed. 2. 3: 277. 1913), Britton (Fl. Bermuda 372. 1918), and Hitchcock & Green (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 131. 1929). Rehder's choice of *L. Xylosteum* appears to be correct.

Early authors treated *Lonicera* in various ways, recognizing one or more genera. Linnaeus (Sp. Pl. 173-175. 1753) placed all the species known to him in one genus, *Lonicera*, with two informal groups, "Periclymenum" and "Chamaecerasus." In contrast, Miller (Gard. Dict. Abr. ed. 4. 1754) distinguished the genera *Caprifolium*, *Lonicera*, *Periclymenum*, and *Xylosteon*. The species of Miller's *Caprifolium* correspond closely with those of Linnaeus's informal group "Periclymenum," and Miller's species 7, *C. italicum* Dod., the Italian honeysuckle, is cited by Linnaeus in the synonymy of *L. Caprifolium*. In 1759 (Gard. Dict. ed. 7), Miller combined *Caprifolium* with *Periclymenum*. In 1768 (Gard. Dict. ed. 8), the full description of *Periclymenum italicum*, as it is called, corresponds exactly with the description of *L. Caprifolium* in *Species Plantarum*. Thus, while maintaining *Lonicera* as a distinct genus, Miller effectively segregated *L. Caprifolium* from *Lonicera* by placing it in his genus *Caprifolium*. This species therefore cannot be used to typify *Lonicera*. In

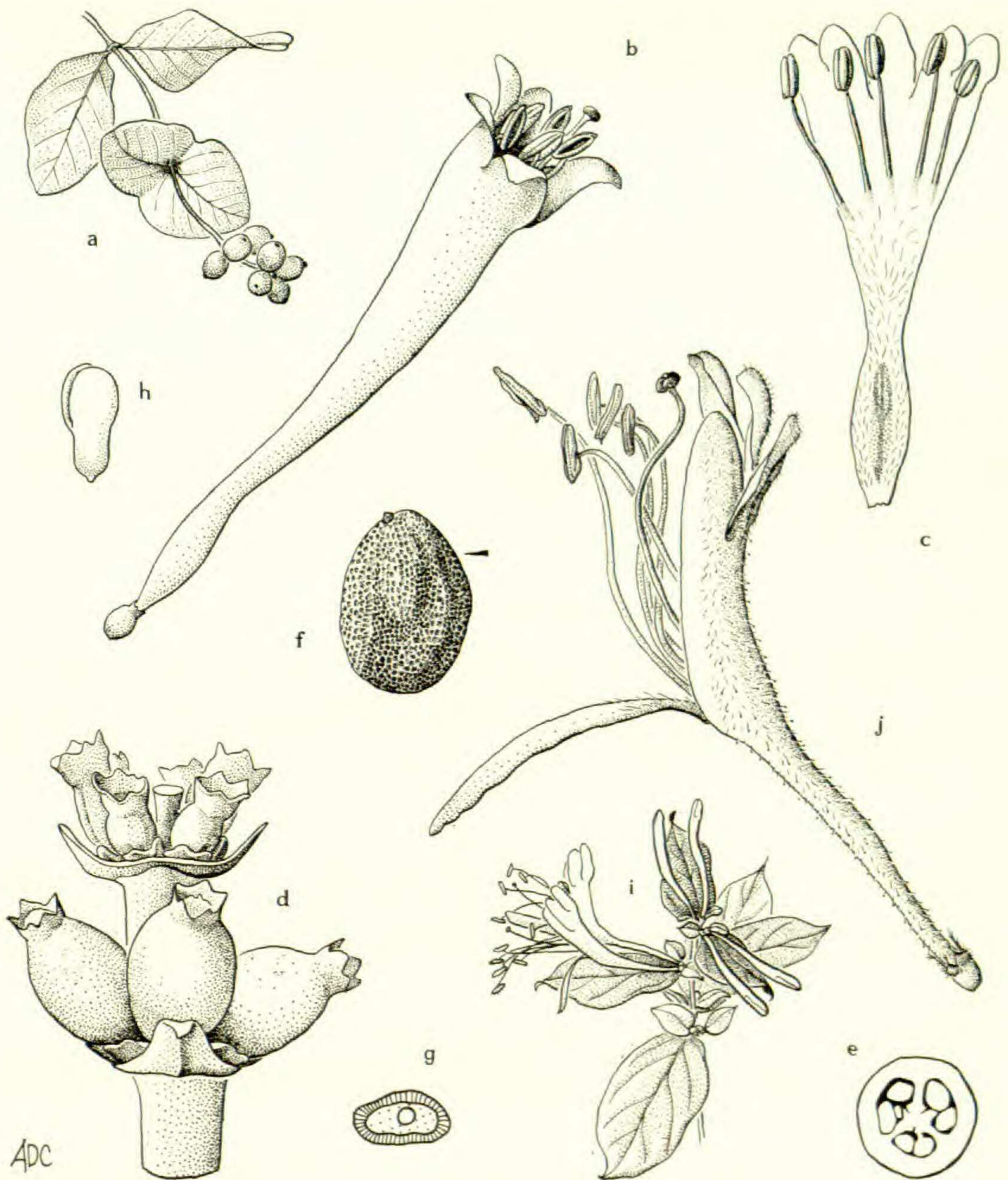


FIG. 3. *Lonicera*. a-h, *L. sempervirens*: a, fruiting branchlet, $\times 1/2$; b, flower, $\times 2$; c, corolla opened lengthwise to show attachment of stamens and distribution of hairs and nectar glands, $\times 1\ 1/2$; d, portion of the inflorescence to show flowers borne in threes — note bracts, bractlets, and ovaries of flowers and buds (corollas removed), $\times 8$; e, ovary in semidiagrammatic cross section to show axile placentation, $\times 10$; f, seed, $\times 6$; g, seed in diagrammatic cross section, showing testa (hatched), endosperm (stippled), and hypocotyl of embryo (unshaded), $\times 6$; h, embryo, $\times 12$. i-j, *L. japonica*: i, flowering branchlet, showing flowers in pairs, $\times 1/2$; j, flower, $\times 2$.

contrast, *L. Xylosteum* was retained by Miller in *Lonicera* throughout. His species 3, "*Lonicera pedunculus bifloris ovatis acutis integris* Lin. Hort. Cliff. The Fly Honey-suckle, vulgo," (Gard. Dict. Abr. ed. 4. 1754) fits Linnaeus's description of *L. Xylosteum* (Sp. Pl. 174. 1753). This was further clarified in 1768 (Gard. Dict. ed. 8), when Miller used the binomial *Lonicera Xylosteum* for this species.

Lonitzer, latinized *Lonicerus*, 1499–1569, a German herbalist and physician, not Adam Lonitzer, 1528–1586; see Linnaeus, *Crit. Bot.* 93. 1737.) — HONEYSUCKLE.

A genus of about 180 species of temperate and tropical regions of the Northern Hemisphere. About 25 species occur in North America; about seven are native in our area and five are introduced. Although Small recognized *Phenianthus* Raf., *Xylosteon* Mill. (*Xylosteon* Juss.), and *Nintooa* Sweet as genera separate from *Lonicera*, there do not seem to be sufficient grounds for adopting this treatment.

The species fall into two well-marked subgenera: *LONICERA* (subg. *Chamaecerasus* Rehd.⁵), distinguished by axillary inflorescences with the flowers in pairs and the leaves free, and *CAPRIFOLIUM* (Mill.) Pers. (subg. *Periclymenum* L., of Rehd.⁵), with terminal, whorled inflorescences of three-flowered cymes and the upper leaves usually connate. The subgenera may be further divided into sections by the regular or irregular corolla, the length of the corolla tube, the climbing or erect habit, and the free or connate bracteoles.⁶

One indigenous and about four introduced taxa of subg. *LONICERA* occur in the southeastern United States. *Lonicera canadensis* Marsh. (*Xylosteon ciliatum* (Muhl.) Pursh), $2n = 18$, a northeastern species extending southward in the mountains to North Carolina, Tennessee, and Georgia, is distinguished by a short, nearly regular corolla distinctly gibbous at the base and by red fruit. *Lonicera japonica* Thunb. (*Nintooa japonica* (Thunb.) Sweet), $2n = 18$, introduced from Asia and now widespread in eastern North America, has become a pernicious and dangerous pest in woodlands, on roadbanks, and in hedgerows, overwhelming and strangling the native flora. An exuberant woody vine, it is readily distinguished by its bilabiate corolla, long-toothed calyx, and black fruits. *Lonicera fragrantissima* Lindl. & Paxton (*Xylosteon fragrantissima* (Lindl. & Paxton) Small), $2n = 18$, a Chinese shrub widely cultivated in the south-

⁵ Rehder (*Missouri Bot. Gard. Rep.* 14: 27–232. 1903) recognized two subgenera: *Chamaecerasus* L. and *Periclymenum* L. As shown in the preceding footnote, however, these were informal categories, not subgenera, under Linnaeus's *Lonicera*. Persoon (*Syn. Pl.* 1: 213. 1805), who appears to be the earliest author to establish subgenera as formal categories in *Lonicera*, distinguished three subgenera: *Xylosteum*, *Caprifolium*, and *Symphoricarpos*. The species placed in subg. *Xylosteum* were very similar to those assigned by Rehder to subg. *Chamaecerasus* and include the lectotype species, *L. Xylosteum*. This should therefore become subg. *Lonicera*. The species in Persoon's subg. *Caprifolium* correspond closely with those in Rehder's *Periclymenum* and include *L. Caprifolium*. *Caprifolium* is the earliest name used in the correct sense at the rank of subgenus and should be adopted.

⁶ Rehder recognized five sections, four within subg. *Lonicera*, but some authors divide the genus only into sections, rather than into subgenera or both subgenera and sections. The sections then usually recognized are *Lonicera*, *Caprifolium* DC., and *Nintooa* (Spach) Maxim., but Warburg (in Clapham, Tutin, & Warburg, *Fl. Brit. Isles*, ed. 2. 790, 791. 1962) mistakenly regarding *L. Caprifolium* as the type species of *Lonicera*, gives the sections as *Xylosteon* (Mill.) DC., *Lonicera*, and *Nintooa* (Spach) Maxim.

eastern United States; *L. Maackii* (Rupr.) Maxim., $2n = 18$, from eastern Asia; and *L. × bella* Zabel (*L. Morrowii* Gray $×$ *L. tatarica* L.), $2n = 18$, are reported to spread from cultivation in our area.

The remaining species in the Southeast are members of subg. CAPRIFOLIUM. *Lonicera sempervirens* L. (*Phenianthus sempervirens* (L.) Raf.), $2n = 36$, of wide range throughout our area, extending north to Maine and west to Nebraska, Ohio, Iowa, and Texas, is distinctive in its slender trumpet-shaped, regular, bright-red corolla. *Lonicera dioica* L., a polymorphic species occurring from Quebec and Maine to British Columbia, Kansas, and Missouri and extending south to North Carolina, Tennessee, and Georgia, is readily recognized by its bilabiate corolla gibbous at the base and uppermost connate leaves green above. The very doubtfully distinct *L. glaucescens* Rydb. is treated as a variety⁷ of *L. dioica* by most authors. *Lonicera flava* Sims, a variable species occurring in the Carolinas, northern Georgia and Alabama, and Tennessee, Kentucky, Missouri, Arkansas, and Oklahoma, is distinguished by its bright orange-yellow bilabiate corolla and elliptic or rhombic, connate uppermost leaves. The paler, somewhat smaller-flowered *L. flavida* Cockerell ex Rehd. is probably best treated as *L. flava* var. *flavescens* Gleason (cf. Steyermark). *Lonicera prolifera* (Kirchner) Rehd. (*L. Sullivantii* Gray), $2n = 18$, closely related to both *L. flava* and *L. dioica*, occurs from Ontario to Wisconsin, Kansas, and Missouri, south to Arkansas and Tennessee. Its nearly orbicular connate uppermost leaves with a glaucous dorsal surface, its extended spicate inflorescence, and its bilabiate pale-yellow corolla gibbous at the base are characteristic. *Lonicera albiflora* Torr. & Gray was described from Fort Towson, Arkansas. Small (in both editions of *Flora of the Southeastern United States*) and Rehder recorded this species from Arkansas, but Fort Towson is today in southeastern Oklahoma, and there appears to be no other record of this species in Arkansas. The European *L. Caprifolium*, $2n = 18$, is reported as an escape from cultivation.

Many of the species are proterandrous. Species with long corolla tubes are pollinated by long-tongued insects or by hummingbirds, while those with short tubes are visited by various Diptera and Hymenoptera. Chromosome numbers of $2n = 18$, 36, and 54 have been reported; most species appear to be diploids ($2n = 18$). A large number of species are grown as ornamentals, and many hybrids (some of them complex) have arisen spontaneously in cultivation.

Lonicera is closely related to *Diervilla* and *Leycesteria*, the three genera showing their affinities in their two- or three-flowered cymes and ovaries with several ovules. *Lonicera* is distinguished from *Leycesteria* by its two- or three-locular *vs.* five-locular ovary and from *Diervilla* by its fleshy fruit.

⁷ Gleason (New Britt. & Brown. 1952) recognized both var. *glaucescens* (Rydb.) Butters and var. *dasygyna* (Rehd.) Gleason. In the event that these varieties are combined (as in Gray's Manual, ed. 8. 1950), the latter name is correct, for it is the older name in the rank of variety, having been described in 1903 under *Lonicera glaucescens*, which itself was not reduced to varietal status until 1913.

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